

# THE EFFECTS OF THE UZU GENE ON PRODUCTIVE TRAITS IN BARLEY

## I. Evaluation of the Genic Effects in Different Genetic Backgrounds

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### I. INTRODUCTION

Cultivated barley is especially rich in conspicuous morphological variations, such as naked kernel, compact head, short culm, reduced or modified lemma appendages, smooth awn, wide glume, etc., which are mostly attributable to simple genic changes from normal to recessive. These gene changes must have been spontaneously arisen and incorporated into the genotypes of cultivated forms probably because of the merits of their major effects for cultural praxis or utility of the products. Moreover, it is possibly considered that, as these mutant forms have survived natural as well as artificial selection for a long period since their occurrence, most of them must be no less productive than those with "normal" genes at least in the regions wherein they are still predominantly cultivated. In sharp contrast to the above thought, however, there have been accumulated in barley and many other kinds of organisms abundant evidence indicating that most of the mutants, both natural and artificial, are more or less inferior in productivity, viability or fecundity to their original forms (Fröier, 1954, Harlan et al. 1940, Scholz 1955, 1957 and 1959, Suneson and Stevens 1957, Suneson and Ramage 1962 for barley).

This apparent contradiction naturally raises an important question: What is the cause that makes the varieties with these mutant genes successful? To approach this problem, it is first of all necessary to evaluate pleiotropic effects of each of these genes on productive traits, and especially to investigate mode of their interactions with different genetic backgrounds and environments.

As was already demonstrated by the authors (Takahashi 1942, Takahashi et al. 1951a, b), a group of barley varieties which have in common a recessive gene called *uzu* (*uz*) are grown widely in Japan, covering about 80 per cent of her whole barley acreage. The effects of the gene *uz* on morphological and ecological features are very conspicuous, which may be summed as follows: Coleoptile length of the *uzu* barley is about one half of that of the normal. Its leaves are shorter, thicker and more erect. Stems, too, are to an extent shorter and thicker, and hence more resistant to lodging. Most of the floral parts, such as rachis internode, awn, rachilla, empty and flowering glumes, anther, etc., are all much reduced in length. Kernels become short, round and plump. Thus, the *uzu* gene exerts

simultaneous diminutive action upon almost all plant parts, though it affects little upon the width. It is also interesting to note that the uzu varieties are confined to central and southern parts of Japan with milder winters. A similar situation is found in Korea. This type of varieties seems not to be established in the other parts of the world, however.

On account of the practical importance and scientific interest, the uzu gene was first chosen as an objective in the proposed series of studies on the genic effects on the productive traits. In this paper are chiefly dealt with the results of study on the effects of uzu gene on yield and its components in a variety of genetic backgrounds.

## II. MATERIALS AND METHODS

A comparative test for genic effects on quantitative characters requires special experimental materials, as variation in environment and genetic backgrounds often masks the genic effects to be investigated. A series of isogenic paired lines, each pair of which differ only in the alleles in question, may be a qualified tool. In developing such isogenic lines three methods are available: (1) to find out a mutant with a change on the locus in question alone, (2) a series of backcrosses to either of the parents after the first cross between two varieties differing in the alleles or (3) selecting plants heterozygous for the alleles continuously among the population in  $F_2$  and succeeding generations until they approach homozygosity for all genes excepting the alleles in question. After this point was reached, two desired type plants are to be isolated in the following segregating generation (see Atkins and Mangelsdorf, 1942). For the technical reason, the third method was adopted, although this method is accompanied by a defect that a few additional genes closely linked with alleles can hardly be released through crossing over.

The outline of the procedure to develop 24 isogenic lines, used in this experiment, is shown in Fig. 1. First, crossings were made between Shanghai-3 and Kobinkatagi and between French-1 and Kobinkatagi. For brevity, the former cross will be named cross A, and the latter cross B. The origin and chief agronomic traits of these three varieties are shown in Table 1. The data shown there were obtained from the measurements on space-planted materials in 1959. The hybrid populations up to their  $F_4$  generation were grown in rows and harvested in bulk. Heterozygotes for *Uzuz* were first selected as many as possible among the space-planted  $F_5$  populations, and in  $F_6$  generation a single heterozygote was taken from each of the  $F_6$  lines. In the following generation, seeds of plants homozygous for *Uz* and those homozygous for *uz*, both derived from a single line, were separated and bulked each, and used for the experiment. Identification of genic constitution for *Uz* and *uz* was quite easily made by a seedling test, because of the marked differences in shape and size of the coleoptiles between normal and uzu individuals (Takahashi 1942). The number of paired lines thus obtained was 14 for cross A and 10 for cross B.

Comparative performance tests with these isogenic pairs were performed for

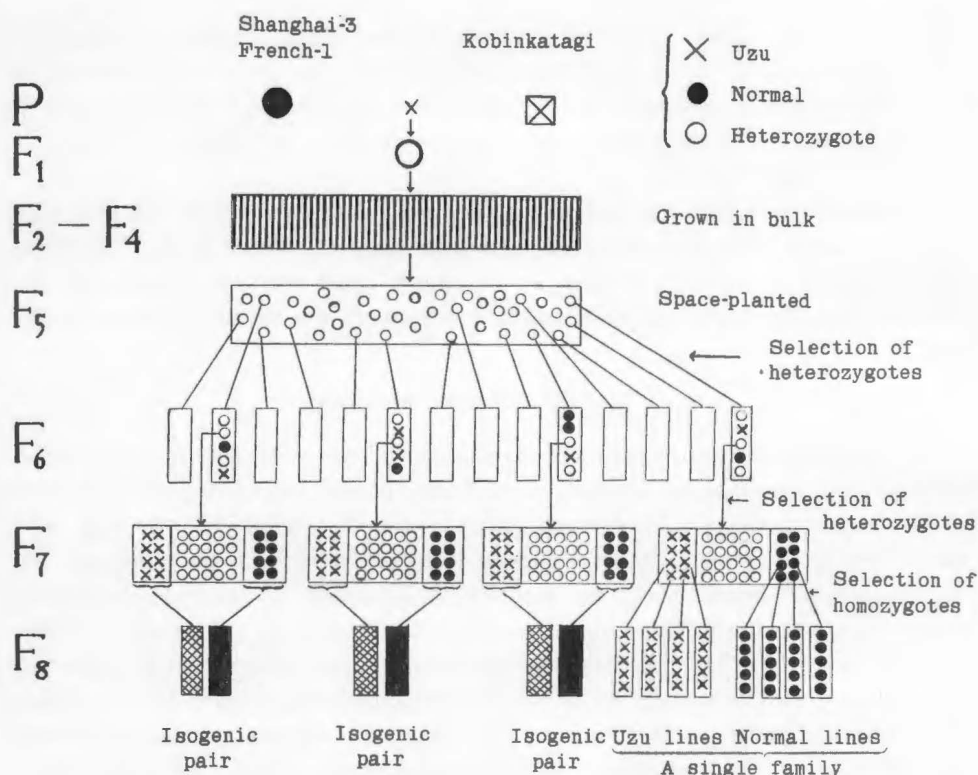


Fig. 1. Procedure of developing Uz-uz isogenic pairs (left 3) and the normal and uzu line groups of a single family (the rightest).

TABLE 1  
Origin and the characteristics of the parental varieties

Variety	Origin	Type	Ear density	Head length (mm)	Stem length (cm)	Number of heads	1000 Grain wt. (g)	Grain wt./pl. (g)	Heading time
Shanghai-3	Central China	Normal	Dense	54	112	14.3	22.5	13.4	Apr. 25
French-1	France	Normal	Lax	85	12	17.7	19.8	17.1	Apr. 29
Kobinkatagi	Hiroshima, Japan	Uzu	Lax	59	10	14.4	22.0	18.4	May 1

two years in 1958~'59 and 1969~'60 (for brevity, designated 1959 and 1960, respectively). The materials used were a total of 24 line pairs, 14 from cross A and 10 from cross B, for the first year's experiment, and 15 pairs, consisting of 14 from cross A and 1 from cross B, for the second year's test. These were planted in a randomized block design with four replicates. Each plot, including the normal and uzu paired lines, were arranged longwise in a row of 3.6 m<sup>2</sup> in size. The seed quantity of each line was determined so as to be securable 320 healthy plants per 1.8 m<sup>2</sup>, based on the results of the preliminary germination test. Records

were taken on a plot basis for grain yield and time of heading. In determining mean values of 1000 grain weight, number of heads per 50 cm row and stem length samples were taken and measured in each plot 3~4, 4 and 6 times, respectively.

### III. EXPERIMENTAL RESULTS AND DISCUSSION

#### 1. *A Test for Variability Within a Family*

It must be admitted that the Uz-uz isogenic pairs to be used in the following experiment have been developed in a hybrid generation too young to attain a state of homozygosis for all genes other than *Uzuz*. So it was thought as necessary to ascertain whether these materials were practically suited for the experimental purpose. Accordingly, a preliminary test for variability within a family was performed with two families derived from two  $F_2$  heterozygous plants taken one each from the cross A and B. Each family consisted of 10 normal lines and 10 uzu lines. They were grown in a randomized block design with four replicates. Each plot consisted of 35 plants, grown 8 cm apart in row.

In Table 2 are shown a summarized result of the analyses of variances for

TABLE 2  
Analysis of variance of the data for three agronomic characters of 10 lines each of the normal and uzu types derived from a single  $F_2$  plant of cross A and B

Source of variation	Degrees of freedom	Yield/ plant		Number of heads		1000 grain weight	
		M. S.	F	M. S.	F	M. S.	F
<i>Cross A</i>							
Within normal	9	1007.79	0.97	700.21	2.90**	3.4870	1.05
Within uzu	9	2519.39	2.43*	238.06	0.98	3.5387	1.06
Normal : uzu	1	69090.01	66.77**	4365.51	18.06**	102.9219	30.86**
Error	57	1034.78		241.70		3.3359	
<i>Cross B</i>							
Within normal	9	913.11	0.74	298.01	1.04	2.0751	0.95
Within uzu	9	1656.01	1.34	191.22	0.67	1.7638	0.81
Normal : uzu	1	36052.58	29.12**	1410.70	4.94*	84.6454	38.72**
Error	57	1238.00		285.50		2.1860	

\* and \*\* exceed 5% and 1% significant levels respectively.

yield per plant, number of heads per plant and 1000 grain weight. The result clearly indicates that there was little variation among either of the normal and uzu lines within a family with respect to the three characters investigated, although in two cases the variance for between lines exceeded 5% or 1% significant level. This may permit to suppose that, even though the isogenics to be used in the following experiment might be to some extent heterozygous for the residual genotypes, the heterozygosis would not impair so much accuracy of the results of comparison. It is also noted in the result that, as far as this isogenic pair is concerned, the normal type was superior in all three characters to the uzu type,

## 2. Comparisons of the Average Effects of the Normal and Uzu Genes on Four Agronomic Traits

Mean values of yield, 1000 grain weight, number of heads per 50 cm row and stem length of 24 normal and uzu paired lines which were each developed from different  $F_6$  heterozygous plants taken from two hybrid populations, and the differences between normal and contrasting uzu lines are shown in the Appendix. Analysis of variance was made of their original data obtained in 1959 and 1960. The results are shown in Table 3 in a rather summarized form. It is quite evident

TABLE 3  
Analysis of variance of four characters indicated of 24 normal and uzu isogenic paired lines derived from two crosses, A and B. Mean squares and levels of significance are indicated

Source		Yield	1000 grain weight	No. of heads	Stem length
Cross A 1959	Within normal type	32855.70**	29.02**	660.36**	226.00**
	Within uzu type	27487.35**	15.11**	889.74**	464.62**
	Normal: uzu	4219.90	47.82**	71.36	9108.04**
Cross B 1959	Within normal type	56933.24**	19.17**	72.33	28.54**
	Within uzu type	48389.06**	11.08**	198.30*	73.57**
	Normal: uzu	0.10	53.35**	1767.20**	3354.11**
	Error	7062.19	1.48	81.39	4.87
Cross A 1960	Within normal type	15832.02**	30.17**	439.61**	423.89**
	Within uzu type	71769.46**	26.72**	667.26**	522.86**
	Normal: uzu	111325.21**	2.43	69.77	13785.22**
	Error	3871.26	0.73	86.65	5.13

\*\* exceeds the 1% level of significance.

\* exceeds the 5% level of significance.

in the table that variations among different lines of both the normal and uzu types are so large and mostly significant at the 1% level, which result is in sharp contrast to those obtained in the previous experiment with the lines derived from a single  $F_6$  plant. This doubtlessly implies a marked difference in the genetic constitutions among these isogenic pairs.

Now suppose these isogenic pairs represent the normal and uzu genes in an average genetic background, comparison of the general means of the normal and uzu lines for each of the characters will permit to determine which of the genes, *Uz* or *uz*, is more advantageous for productivity etc. In Table 4 is shown the result. The significant level of the differences indicated were determined by analysis of variance of the data (Table 3).

According to Table 4, the normal type exceeded to some extent the uzu type regarding stem length, grain yield and also 1000 grain weight, and the difference in stem length proved to be statistically significant in all comparisons. But, the differences in the latter two characters were not so marked and insignificant in a specific year or cross. The results of the number of heads per 50 cm row varied with crosses; the normal type from cross A was slightly more than the corres-

TABLE 4

General means of grain yield, 1000 grain weight, number of heads per 50 cm row and stem length of the normal and uzu type lines, and their differences

		Yield (g/plot)	1000 grain weight (g)	No. of heads (50 cm row)	Stem length (cm)
Cross A 1959	Normal	934.4	18.92	126.1	112.1
	Uzu	895.6	17.61	124.5	94.1
	Difference	38.8	1.31**	1.6	18.0**
Cross B 1959	Normal	896.3	16.80	139.3	115.1
	Uzu	896.1	15.18	148.7	102.1
	Difference	0.2	1.62**	-9.4**	13.0**
Cross A 1960	Normal	962.7	20.66	151.8	114.4
	Uzu	901.8	20.38	150.3	92.9
	Difference	60.9**	0.28	1.5	21.5**

\*\* exceeds the 1% level of significance.

ponding uzu type, while the relation was quite reverse with those from cross B.

The writer have ever made an experiment in order to know the changes in relative frequencies of three recessive genes, *uz*, *l*, and *n* for semi-brachytic growth, compact head and naked kernel, respectively, in the segregating populations of several crosses, and at the same time to evaluate the effects of these genes on productive traits. The result was such that uzu type plants were badly eliminated from all the populations in every generations, and moreover, they were much inferior to the normal in yield, 1000 grain weight and number of heads per plant. The apparent discrepancy between these two results might have chiefly been resulted from the difference in experimental procedure: In the former experiment the normal and uzu plants were grown in mixture and accordingly competitive effects between two types, besides their genic effects, markedly affected the results. Judging from these results hitherto obtained, the gene *uz* definitely decreases stem length, and at the same time it seems to affect yield and grain weight disadvantageously in some degree.

### 3. Variation among Isogenics in the Differences between the Normal and Uzu Paired Lines.

A glance at the Appendix immediately shows that the differences in various characters between the normal and uzu paired lines vary considerably with isogenics. The difference (normal minus uzu) in the grain yield, for instance, is very large and positive in some pairs, it is only slight in some and it is negative in some others. As this was thought as important and worthy of examination on practical and scientific viewpoint, analysis of variance of the data was made in order to determine whether these differences in each of the characters between the normal and uzu lines among isogenics are statistically significant. The result shown in Table 5 indicates that the isogenics differed significantly in the differences between



normal and uzu pair at mostly 1 per cent level with only a few exceptions. This may suggest the Uz-uz line differences being largely under the genetical control.

TABLE 5  
Analysis of variance for the Uz-uz differences in four characters indicated.  
Mean squares and significant level alone are shown

Source of variation		Differences between normal and uzu paired lines in			
		Grain weight	1000 kernel wts.	Head number	Stem length
1959	Between isogenics from cross A	33580.67**	7.3531**	458.62**	82.694**
	Between isogenics from cross B	7936.93	5.0094*	158.89	30.606**
	Error	11275.20	2.4243	152.04	7.758
1960	Between isogenics (A)	50255.77**	7.6318**	250.39	65.627**
	Error	5767.76	0.8272	191.15	5.945

\*\* 1% level of significance, \* 5% level of significance.

TABLE 6  
Interrelationships among the values of each of the four characters, namely, yield, 1000 grain weight, number of heads and stem length, of the normal and uzu lines and their differences, expressed in terms of coefficient of correlation between either two of these three items. D and L stand for the dense eared and lax-eared isogenics, respectively

Character	Cross Year	Between norm. & uzu	Between normal & "difference"	Between uzu & "difference"
Yield	A	1959 0.445	0.586* { D. 0.613 L. 0.275	-0.463 { D. -0.075 L. -0.458
		1960 0.554*	-0.143 { D. -0.216 L. 0.096	-0.884** { D. -0.717* L. -0.879*
	B	1959 0.928**	0.388	0.155
1000 grain weight	A	1959 0.865**	0.520 { D. 0.886** L. 0.045	0.279 { D. 0.624 L. -0.305
		1960 0.869**	0.365 { D. 0.876** L. 0.298	-0.147 { D. 0.796* L. -0.182
	B	1959 0.931**	0.659**	0.187
Number of heads	A	1959 0.702**	0.127 { D. 0.263 L. 0.376	-0.617* { D. -0.364 L. -0.672
		1960 0.791**	0.034 { D. 0.394 L. -0.634	-0.585** { D. -0.524 L. -0.861*
	B	1959 0.461	0.159	-0.803**
Stem length	A	1959 0.944**	-0.579* { D. 0.204 L. -0.095	-0.822** { D. -0.626 L. -0.866*
		1960 0.936**	-0.316 { D. 0.194 L. 0.468	-0.444 { D. -0.487 L. -0.332
	B	1959 0.665*	-0.244	-0.679*

\* exceeds the 5% level of significance.

\*\* exceeds the 1% level of significance.

#### 4. *Inquiry into the Nature and Cause of the Differential Interactions of the Genes, Uz and uz, with the Genetic Backgrounds*

Since Uz-uz isogenic paired lines are expected to differ with each other only in the alleles *Uz* and *uz* but possess the same genetic background, the phenotypic difference between the normal and uzu lines should be the same in all the isogenic pairs, unless the alleles *Uz* and *uz* exert interaction with different genetic backgrounds. However, the real state of things was, as shown in the previous section, quite different: there were marked difference among isogenic pairs. It is therefore reasonable to consider that the normal and uzu differences among isogenics are due to the differential interactions of *Uz* and *uz* with the genetic backgrounds involved in different isogenics. Now it becomes our keen interest to gather information about the nature and cause of such a differential interaction. A clue to the solution of the proposed problem may probably be given by investigating the interrelationships among the values of each character of the normal and uzu lines and their differences. In Table 6 are given the coefficients of correlation between either two of these three items.

According to Table 6, close positive correlations existed between the values of the normal and uzu lines for all of the characters investigated. This is quite a natural outcome, inasmuch as each of the paired lines not only possessed of the

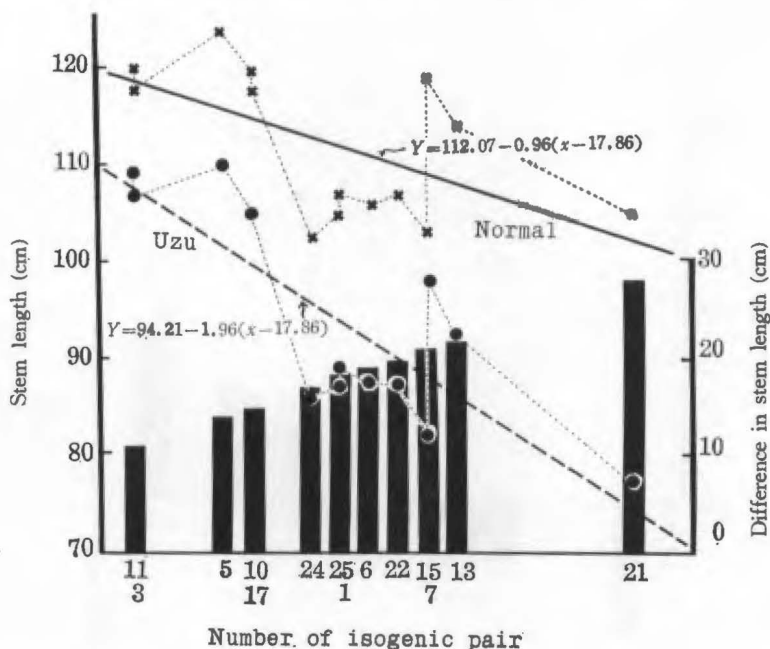


Fig. 2. Stem lengths of the normal and uzu isogenic lines and their differences of the 14 isogenics from cross A grown in 1959, as arranged according to the magnitude of the differences in isogenic pair.



same genetic background in common, but they have been grown side by side, and hence both genetic and environmental correlations might have contributed to the phenotypic ones.

On the other hand, as the differences in the four characters between the normal and uzu lines are determined by both the values of the normal and uzu lines, the relations with the latter two are expected to be somewhat complicated. Table 6 shows that the differences (normal minus uzu lines) in stem length correlate inversely with both the values of the normal and uzu lines, regardless of years and crosses, but the coefficients of correlations with uzu's are always higher than those with the normals. Fig. 2 may help to visualize their relations. In this figure, in which are shown the actual data for the isogenics from cross A tested in 1959, 14 isogenics were arranged from right to left in the order of magnitude of the Uz-uz line difference, and the stem length of the normal and uzu lines and their difference in each isogenic pair are plotted. It is perceived easily that the uzu lines are apparently more variable and represent a more acute slope of regression line than the normal lines.

The results of similar analyses made of the two years' data of the grain yield are shown in Figs. 3 and 4, and also in Table 6. These clearly indicate that the differences in yield of the isogenic pairs from cross A in 1959 and 1960 correlated inversely with the yield of the uzu lines, although its correlation with the yield of

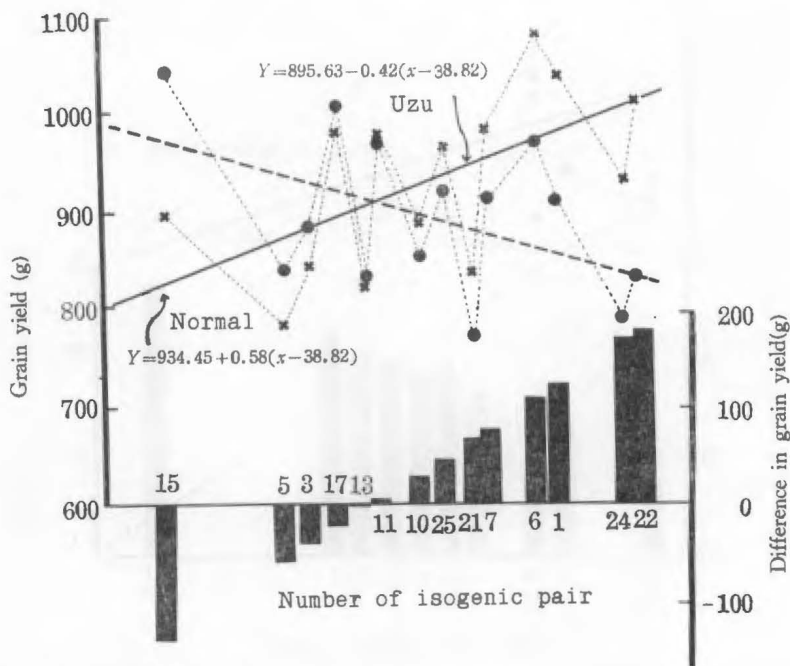


Fig. 3. Yields of the normal and uzu lines and their differences of the 14 isogenic pairs from cross A grown in 1959, as arranged in the order of magnitude of the differences between normal and uzu lines.

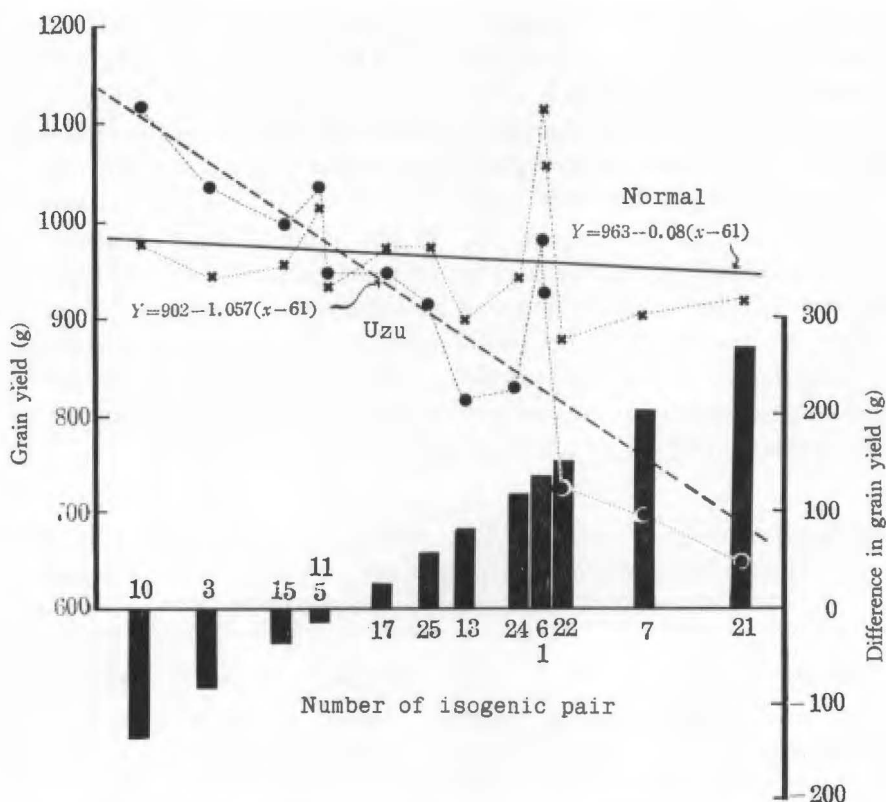


Fig. 4. Yields of the normal and uzu lines and their differences of 14 isogenic pairs from cross A grown in 1960, as arranged according to the magnitude of the difference in isogenic pair.

the normals was significantly positive in 1959, but it was slight in 1960. As for the isogenics from cross B, no definite relations were ascertained. The results as to head number were substantially the same as those for the yield of the isogenics of cross A in 1960: The correlation coefficients of the "difference" with the number of head of the uzu lines were always significantly negative, but those with the values of the normal lines were only slight. These results may be explained on the basis that the gene *uz* has interacted with the genetic backgrounds more intensely than the gene *Uz*, or inversely that the plus or minus effects of the genetic backgrounds have been intensified in the presence of *uz* more than that exhibited by the same genetic backgrounds in cooperation with *Uz*.

The results of 1000 grain weight are somewhat different from those of three other characters: There seems to be a slight tendency that the differences between normal and uzu lines increase with the rise of the values of the normal lines, but are rather indifferent of the values of the uzu lines.

In the course of this analytical study the writers became aware of another interesting fact that the magnitude of the *Uz-uz* differences in these characters

among isogenics might be conditioned to a considerable extent by the gene pair *Ll* for lax and dense ear. As already shown in Table 1, cross A is a hybrid between dense-eared (Shanghai-3) and lax-eared varieties (Kobinkatagi), while cross B is a hybrid between lax-eared parents. So it is expected that in the later segregating generations of the former hybrid lax and dense eared forms will appear in a 1 : 1 ratio, if the ear density is, as is the case for the most East-Asian barleys, governed by a single pair of gene, *Ll*. In fact, 8 out of the 14 isogenics, which had been randomly taken from a  $F_2$  hybrid population, were found to be of dense-eared type and the remaining 6 to be of lax-eared one. Accordingly, it was possible to classify the lines derived from cross A into four distinct groups, namely, normal-lax, normal-dense, uzu-lax and uzu-dense, and to compare the effects of the genes *L* and *l* for ear density in the presence of either *Uz* or *uz* on the characters investigated. Table 7 gives the summarized result.

TABLE 7

Comparison of mean values of yield, 1000 grain weight, number of heads and stem length among four plant types: normal-lax eared, normal-dense-eared, uzu lax-eared, and uzu-dense-eared

Character	Item	1959			1960		
		Lax	Dense	Difference	Lax	Dense	Difference
1. Grain yield	Normal	895.13	963.94	-68.81	966.88	961.56	5.32
	Uzu	934.25	866.66	67.59	1009.17	815.00	194.17*
	Difference	-39.12	97.28**		-42.29	146.56**	
2. 1000 K. W.	Normal	19.46	18.52	0.94	21.08	20.77	0.31
	Uzu	17.52	17.69	-0.17	21.95	19.50	2.45
	Difference	1.94**	0.83		-0.87	1.27**	
3. Head number	Normal	130.67	122.75	7.92	155.33	147.63	7.70
	Uzu	134.17	117.50	16.67*	152.33	147.38	4.95
	Difference	-3.50	5.25		3.00	0.25	
4. Stem length	Normal	119.79	106.31	13.48	124.67	106.25	18.42
	Uzu	105.08	85.78	19.30	104.50	84.00	20.50
	Difference	14.71**	20.53**		20.17**	22.25**	

\* exceeds the 5% level of significance.

\*\* exceeds the 1% level of significance.

Comparisons of the lax and dense eared types in both the normal and uzu groups reveal that the dense-eared type is inferior to the lax-eared one in most cases, and disadvantage of dense-eared type is more marked in the uzu group than in the normal group. This is doubtlessly due to the fact that doubly recessive or uzu-dense type is by far worse than others regarding all the characters with no exception. It may therefore be reasonable to consider that the gene *l* for dense ear has exerted unfavorable effects upon these traits, and when combined with the gene *uz*, its unfavorable effects have been still more intensified.

The writers (Takahashi et al. 1958) have obtained quite a similar result in the previous study on the changes in gene frequencies in some hybrid populations. Namely, it was recognized that the dense-eared uzu type plants had mostly been eliminated from the populations in every generations, and moreover, its yield and 1000 grain weight were always very low as compared with those of three other types. As another example of the same kind, a result of study on interaction of *Uzuz* with *Brbr* for normal vs. brachytic growth can be illustrated (Takahashi and Hayashi, 1956). In this experiment, the doubly recessive type, called br-uz, was found to be as short in the lengths of stem, awn etc. as only about one eighth to one tenth of the singly recessive, uzu and brachytic types, the latter two being almost similar in their lengths. The weight and size of grains of br-uz were also considerably reduced, though not so much as in stem length.

It seemed, however, that the genes *Ll* were not the unique ones that interacted with *Uz* and *uz*, but a number of inseparable genes with minor effects in the genetic backgrounds might have had a share to some extent in the differential interactions. In order to show the situation, correlation coefficients between normal- and uzu-line differences and the values of the normal and uzu lines were calculated separately within dense-eared group and also lax-eared group of cross A, as this treatment might be effective to exclude the effects of the genes *Ll*. For the isogenics from cross B such treatment was not needed, however. The results are shown in Table 5, which indicate that the coefficients of correlation thus obtained for both groups are not much different from those obtained from the bulked data with respect to the characters other than 1000 grain weight.

These may be interpreted to show that a group of genes with minor effects, too, have interacted with *uz* more strongly than with *Uz*. The results for 1000 grain weight were entirely different, namely, very high positive coefficients of correlation were obtained within dense-eared group, especially of normal type, while no such relations were seen within the lax-eared group. This may be explained on the assumption that the effects of the minor genes distributed in different isogenics have become recognizable only in the presence of the gene *l* for dense ear.

##### 5. *Correlation of the Difference between Normal and Uzu Lines in Yield and 1000 Grain Weight with Mean Stem Length of each Isogenic Pair*

Interrelationships among different characters and the character-differences between the normal and uzu lines constitute another problem of interest. In Table 8 are shown coefficients of correlations of different combinations of means of stem length, yield and 1000 grain weight of isogenic pairs and their normal—uzu differences which were calculated from the data of 14 isogenics from cross A.

It is most interesting to note in this result that considerably high, significant negative correlation exists between the yield difference and mean stem length. The relation will be visualized more obviously by a scatter diagram for two years' average data, which is shown in Fig. 5. Now suppose average of the values of the normal and uzu pair represent relative effectiveness of the genetic background

TABLE 8  
Interrelationships among means of yield, stem length and 1000 grain weight  
of each of isogenic pairs and differences between the normal and uzu  
paired lines in these three characters

	Year	Yield	Stem length	1000 gr. weight	Yield difference	Stem lgth. difference
Stem length	{ 1959	-0.082				
	{ 1960	0.665**				
1000 grain weight	{ 1959	0.468	0.294			
	{ 1960	0.265	0.204			
Difference in yield	{ 1959		-0.735**	0.116		
	{ 1960		-0.951**	-0.102		
Difference in stem length	{ 1959	-0.199		-0.383	0.247	
	{ 1960	-0.444		-0.469	0.404	
Difference in 1000 grain weight	{ 1959	0.239	0.038		-0.031	-0.652**
	{ 1960	-0.458	-0.836**		0.793**	-0.071

\* exceeds the 5% significant level.

\*\* exceeds the 1% significant level.

of each isogenic pair on the characters under consideration, the result would signify that the genetic background which have favored elongation of stem length have reduced the difference in yield at the same time: in other words, the taller an isogenic pair is, the more the yield of the uzu line approximates to the yield of the corresponding normal line. This statement may also be applicable for the isogenics of dense-eared group, as the coefficient of correlation within this group is as high as  $-0.911$ . However, such a relation appears no longer existing within the lax-eared group of isogenics: the correlation coefficient is  $+0.051$  for within lax-eared isogenics of cross A, and it is  $0.545$  for the isogenics of cross B, both of which are statistically insignificant.

The result above stated does not necessarily signify the close association of yield with stem length. Instead, the correlation between mean yield and mean stem length was  $+0.665$  for the data in 1960 and it was very low for those in 1959, both being insignificant. Actual situation can be seen in Fig. 6, in which are represented two years' averaged data in a diagramatic way. It is apparent that the lax-eared (=long-stemmed) isogenics are mostly high yielders, while majority of the dense-eared (=short-stemmed) ones are low yielders, but in both groups there are several exceptions. Namely, lines No. 1, 6, and 25 are comparatively high in yield as compared with the other dense-eared lines, and line No. 5, on the contrary, is much lower in yield than the other lax-eared lines. The relation appears very interesting as it suggests some genes or gene complex responsible for yield being involved besides those affecting both plant height and yield simultaneously.

It seems difficult to draw a definite conclusion as to the relation between stem length and the normal-uzu line difference in 1000 grain weight, because of the inconsistency of two years' results, namely coefficient of correlation for 1959

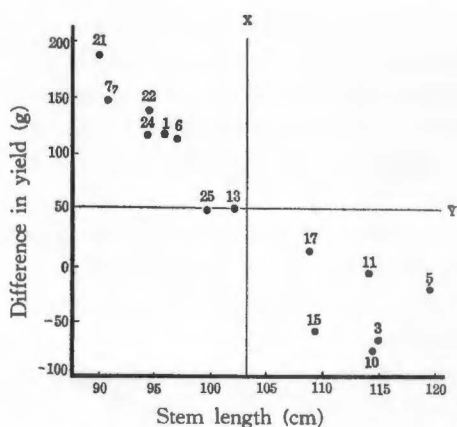


Fig. 5. A scatter diagram showing the relation of stem length with the difference in yield between the normal and uzu lines, based on two years' average data of the isogenics derived from cross A.

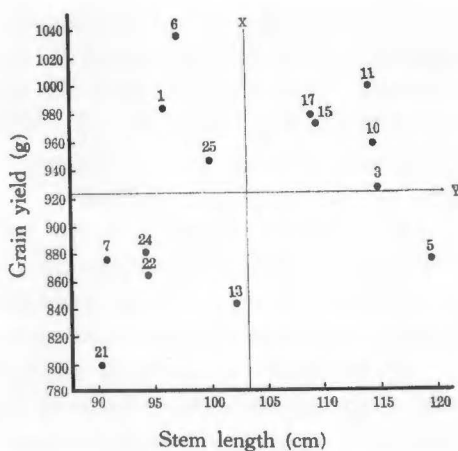


Fig. 6. A scatter diagram showing the relation between stem length and yield, based on two years' average data of the isogenics derived from cross A.

data is very low, whereas it is as high as  $-0.836$  for 1960. Nevertheless, it was found that almost similar relations were existing between two years data when dense-eared isogenic group and lax-eared one were separately treated. Namely, the data of the dense-eared group obtained in 1959 and 1960 gave high adverse coefficients of correlation, namely,  $-0.889$  and  $-0.898$ , respectively, while the data of the lax-eared group did  $+0.560$  and  $+0.370$ , which were almost similar to the estimate,  $+0.515$ , that was obtained from the data of 10 paired lines of cross B. It is hard to consider that such coincidence of two years' results has occurred by chance, and especially so it is not, as these relations thus found are quite similar to the relations of the "difference" in yield with stem length, which were confirmed within dense-eared and lax-eared groups. The latter fact leads further to a supposition that the data of cross A in 1960, but not the data of 1959, might represent the normal state of their relation, though there is no evidence in support of this supposition. If this be true, it follows that genes or gene complex responsible for stem length might have affected simultaneously the difference between normal and uzu lines in both yield and 1000 grain weight, and further that a high positive correlation will be expected between the differences in 1000 grain weight and the differences in yield. From the actual data in 1960 as high a coefficient of correlation as  $+0.793$  was obtained.

#### SUMMARY

In view of the practical importance of the gene *uz* in barley breeding in Japan, a study was made to determine how and to what extent the gene exerts pleiotropic effects on yield and its components. Special attention was paid to its interaction



with the different genetic backgrounds which cooperate with the gene in character expression. Twenty four normal-uzu isogenic pairs, each differing only in *Uz* and *uz* alleles, were developed from the heterozygous plants in the  $F_2$  hybrid generation of two crosses, Shanghai—3  $\times$  Kobinkatagi (cross A) and French—1  $\times$  Kobinkatagi (cross B), and used as the materials. Results of the two years' tests with them may be summed as follows :

1) As was expected from the previous results (Takahashi 1942), the gene *uz* proved to exert marked diminutive effect on stem length. It also brought about decrease, though slight, in grain yield and weight in an average genetic background. Its effect on number of heads was rather ambiguous.

2) However, interactions of *Uz* and *uz* with genetic background were so marked that the differences between normal and uzu pairs in stem length, yield, 1000 grain weight and number of heads were considerably different with isogenic pairs. Consequently, with respect to yield and 1000 grain weight, for instance, normal lines exceeded their contrasting uzu lines in some isogenics, but in some other pairs uzu lines surpassed the normals.

3) Such normal-uzu differences in stem length, yield and head number seemed to be due to the interaction of *uz* with genetic backgrounds being stronger than that of the gene *Uz* with the same genetic backgrounds. With respect to 1000 grain weight, on the other hand, *Uz* seemed to interact with genetic background stronger than *uz*.

4) It was shown further that such a differential interactions of *Uz* and *uz* with genetic backgrounds might have been resulted from the differences in the genotypes of these isogenic pairs, especially in the alleles, *L* and *l*, for lax and dense ear and also a group of genes with minor effects.

5) It was found a high adverse correlation existing between stem length and the normal-uzu line differences in yield and probably also in 1,000 grain weight, which suggested that some genes or gene complex responsible for stem length interacted differently with the genes, *Uz* and *uz*. It seems however, that yield was not affected solely by the genes or gene complex above stated, but was affected also by some other genes.

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## Appendix

Means of (1) yield, (2) 1000 grain weight, (3) number of heads per 50 cm row, and (4) stem length and their differences of 24 normal and uzu paired lines derived from two crosses. Lines, No. 3—17 indicated in upper half are of lax eared type, and lines No. 1—25 in lower half of dense-eared type

## (1) Yield:

Line	Cross A (1959)			Cross A (1960)			Cross B (1959)			
	Normal	Uzu	Differ.	Normal	Uzu	Differ.	Line	Normal	Uzu	Differ.
3	844	888	-44	941	1029	- 88	2	772	760	12
5	780	840	-60	935	945	- 10	4	1001	995	6
10	886	854	32	979	1114	-135	9	1126	1094	32
11	977	972	5	1020	1033	- 13	12	755	760	- 5
15	900	1042	-142	955	994	- 39	14	879	909	- 30
17	986	1010	-24	971	941	330	16	952	949	3
							18	793	899	-106
1	1041	915	126	1060	921	139	(18)	(946)	(951)	(- 5)
6	1081	970	111	1116	979	137	19	839	779	60
7	985	908	77	903	698	205	20	853	855	- 2
13	826	830	-4	900	815	85	23	995	963	32
21	830	761	69	916	644	272				
22	1014	835	179	879	728	151				
24	962	790	172	945	824	121				
25	973	925	48	974	913	61				

## (2) Number of heads per 50 cm row:

Line	Cross A (1959)			Cross A (1960)			Cross B (1959)			
	Normal	Uzu	Differ.	Normal	Uzu	Differ.	Line	Normal	Uzu	Differ.
3	131	134	- 3	156	161	- 5	2	138	153	-15
5	120	127	- 7	141	131	10	4	140	151	-11
10	131	143	-12	168	170	- 2	9	140	136	4
11	125	145	-20	159	163	- 4	12	135	141	- 6
15	150	144	6	165	158	7	14	135	149	-14
17	127	112	15	143	131	12	16	140	158	-18
							18	146	154	- 8
1	131	126	5	154	156	- 2	(18)	(163)	(161)	(2)
6	116	121	- 5	143	143	0	19	137	151	-14
7	112	113	- 1	142	158	-16	20	147	153	- 6
13	115	99	16	146	144	2	23	135	141	- 6
21	136	118	18	151	148	3				
22	104	100	4	132	127	5				
24	135	133	2	150	155	- 5				
25	133	130	3	163	148	15				

## (3) 1000 grain weight (g)

Line	Cross A (1959)			Cross A (1960)			Cross B (1959)			
	Normal	Uzu	Differ.	Normal	Uzu	Differ.	Line	Normal	Uzu	Differ.
3	20.83	18.06	2.77	21.68	23.31	-1.63	2	14.80	12.98	1.82
5	20.53	17.73	2.80	22.41	23.95	-1.54	4	18.99	16.58	2.41
10	16.64	14.69	1.95	18.08	19.77	-1.69	9	19.87	18.51	1.36
11	20.79	19.09	1.70	23.15	22.00	1.15	12	13.86	13.77	0.09
15	16.80	15.12	1.68	18.41	18.81	-0.40	14	16.79	15.63	1.16
17	21.14	20.41	0.73	22.76	23.84	-1.08	16	17.73	15.92	1.81
							18	13.79	13.60	0.19
1	18.06	16.80	1.26	20.70	19.42	1.28	(18)	(17.23)	(17.96)	(-0.73)
6	20.82	19.42	1.40	24.79	23.15	1.64	19	18.72	14.64	4.08
7	23.38	20.86	2.52	24.92	22.49	2.43	20	15.57	14.12	1.45
13	15.68	16.69	-1.01	17.43	16.77	0.66	23	17.87	16.13	1.74
21	14.14	16.06	-1.92	17.19	16.31	0.78				
22	21.52	19.14	2.38	22.36	20.33	2.03				
24	17.66	15.77	1.89	20.70	19.49	1.21				
25	16.92	16.77	0.15	18.19	18.04	0.15				

## (4) Stem length (cm)

Line	Cross A (1959)			Cross A (1960)			Cross B (1959)			
	Normal	Uzu	Differ.	Normal	Uzu	Differ.	Line	Normal	Uzu	Differ.
3	118	107	11	126	109	17	2	117	99	18
5	124	110	14	135	110	25	4	117	106	11
10	120	105	15	126	106	20	9	117	103	14
11	120	109	11	120	107	13	12	115	104	11
15	119	98	21	123	98	25	14	113	99	14
17	118	103	15	118	97	21	16	110	99	11
							18	112	98	14
1	105	87	18	116	86	20	(18)	(117)	(97)	(20)
6	106	87	19	109	87	22	19	118	109	9
7	103	82	21	100	78	22	20	118	108	10
13	114	92	22	114	89	25	23	115	98	17
21	105	77	28	104	74	30				
22	107	87	20	101	83	18				
24	103	86	17	104	84	20				
25	107	89	18	112	91	21				